

THE DEFINITION OF LEAF CONSISTENCE CATEGORIES IN THE FYNBOS BIOME AND THEIR DISTRIBUTION ALONG AN ALTITUDINAL GRADIENT IN THE SOUTH EASTERN CAPE

R. M. COWLING

(Department of Botany, University of Cape Town, Private Bag, Rondebosch 7700, R.S.A.)

B. M. CAMPBELL*

(Botanical Research Unit, P.O. Box 471, Stellenbosch 7600, R.S.A.)

ABSTRACT

Leaf consistence is a morphological feature which is used as an attribute for the structural classification of communities and for the evolutionary interpretation of plant form and function. There are, however, no unambiguous criteria for the characterisation of leaf consistence categories. In this paper criteria for the subjective categorisation of leaf consistence by "feel" are tested by determining indexes of sclerophylly and succulence on leaves classed on a *a priori* basis as sclerophyll, orthophyll, fleshy (semi-succulent) or succulent. Results show differences in degree of sclerophylly (leaf dry weight per unit leaf area) and degree of succulence (maximal water content per unit leaf area) among the subjectively determined categories. The adaptive significance of the leaf consistence categories is indicated by direct gradient analysis of two parallel transects in the south eastern Cape, one in fynbos, the other in non-fynbos vegetation. In non-fynbos changes in leaf consistence along the gradient are interpreted largely as a response to changes in climate and soil moisture. We interpret the predominance of sclerophyll leaves throughout the fynbos gradient as a response to low soil fertility.

UITREKSEL

DEFINIERING VAN BLAARSTRUKTUUR-KATEGORIEË IN DIE FYNBOS BIOOM EN DIE VERSPREIDING DAARVAN LANGS 'N HOOGTE GRADIENT IN DIE SUIDOOS-KAAP

Blaarstruktuur as 'n morfologiese kenmerk word gebruik vir die klassifikasie van gemeenskappe en die evolusionêre interpretasie van plantvorm en funksie. Daar bestaan egter geen duidelike kriteria vir die subjektiewe indeling van blaarstruktuurkategorieë nie. In hierdie artikel word die subjektiewe indeling van blaarstruktuur deur die "voel" metode getoets deur indekse van sklerofilie en sukkulensie van blare op 'n *a priori* basis as sklerofil, orthofil, vlesig of sukkulent aangegee. Resultate toon 'n verskil in die graad van sklerofilie (blaar droë gewig per eenheid blaar oppervlakte) en graad van sukkulensie (maksimale water inhoud per eenheid blaar oppervlakte) onder die subjektief bepaalde kategorieë. Die aanpasbaarheidsbetekenis van blaarstruktuur-kategorieë is aangedui deur 'n direkte gradient ontleding van twee parallel-

* Present address: University of Zimbabwe, Harare, Zimbabwe.

Accepted for publication 12th November, 1982

le transekte in die Suidoos-Kaap, een in fynbos en die ander in nie-fynbos plante-groei. In nie-fynbos kan die veranderings interpreteer word as 'n reaksie op klimaats-en grondvog. Ons interpreteer die oorwegende sklerofille blaar-voorkoms in die fynbos gradient as 'n reaksie op die lae grondvrugbaarheid.

INTRODUCTION

Consistence is here defined to refer to both the firmness and thickness of a leaf (see Werger and Ellenbroek, 1978). This leaf characteristic has long been cited as a structural feature which correlates well with the regional climatic regime (e.g. Schimper, 1903). The adaptive significance of leaf consistence has been the focus of a number of studies (Loveless, 1962; Beadle, 1966; 1968; Small, 1972; 1973; Orians and Solbrig, 1977; Werger and Ellenbroek, 1978; Camerik and Werger, 1980; Bond, 1981), while leaf consistence *per se* is used as an attribute for structural classification with purely phytosociological objectives (Webb, Tracey, Williams and Lance, 1970; Bond, 1981). The definition of leaf consistence categories, however, and their recognition in the field, remains problematic (Loveless, 1962; Small, 1973; Beadle, 1966; Bond, 1981).

Leaf consistence grades from an orthophyll or soft-leaved type towards increasing sclerophyllly. All categories are subjective and cannot be sharply defined by any standards (Beadle, 1966). Students of vegetation in the Fynbos Biome (Kruger, 1978) have achieved some measure of agreement on a subjective classification of leaf consistence types based on "feel" (Bond, 1981: Table 1). Here we provide a test for the subjective criteria used in this scheme (see Table 1) by determining indexes of sclerophyllly and succulence (Camerik and Werger, 1980) on leaves, categorised on an *a priori* basis as orthophyll, sclerophyll, fleshy (semi-succulent) or succulent.

Direct gradient analysis (Whittaker, 1967) has proved to be an effective tool in highlighting the relations of plant community structure to environment (Mooney and Harrison, 1972; Mooney, Gulmon and Parsons, 1974; Parsons and Moldenke, 1975; Werger and Ellenbroek, 1978; Cowling and Campbell, 1980; Bond, 1981). We briefly indicate the adaptive significance of leaf consistence by examining the relative importance of consistence categories along parallel altitudinal gradients in fynbos and non-fynbos vegetation in the south eastern Cape.

MATERIAL AND METHODS

Consistence determination

Branches were sampled from a range of species subjectively classed into consistence categories (Table 4) by ourselves in the field. All samples were collected at 11h00 in mid-December from species growing in the National Botanic Gardens, Kirstenbosch. Soil type and microclimate were regarded

TABLE 1.

Subjective categorisation of leaf consistence by "feel" [adapted from Bond (1981)].

Texture	Characterisation and examples
Succulent	Leaves turgid, express copious liquid when squeezed between thumb and forefinger <i>Delosperma</i> , <i>Mesembryanthemum</i> , <i>Crassula</i> , <i>Euphorbia mauritanica</i>
Fleshy (Semi-succulent)	Leaves usually pulpy, little liquid expressed but leaves collapse with a rubbery or gelatinous texture when rolled between thumb and forefinger <i>Relbunium genistaefolia</i> , <i>Chrysocoma tenuifolia</i> , <i>Pteronia fasciata</i> , <i>Felicia filifolia</i>
Sclerophyll	Leaves hard, coriaceous and thick, breaking when folded <i>Protea</i> , <i>Phyllaea</i> , <i>Passerina</i> , <i>Sideroxylon inerme</i>
Orthophyll	Leaves soft, thin and pliant when folded <i>Ocotlea bullata</i> , <i>Clusia pulchella</i> , <i>Gnidia coriacea</i> , <i>Indigofera denudata</i>

as uniform for the whole sample. No visible signs of leaf chlorosis or flaccidity were noted.

Sampled branches were sealed in plastic bags and immediately transported to the laboratory. Ten leaves were selected from each species and submerged in a container of distilled water and kept in a dark coldroom (10 °C) for 24 h to achieve maximum hydration. The next day fresh mass and the surface area of each leaf were determined. Dry mass was determined by oven-drying the leaves at 105 °C for 24 h. With these data the following parameters could be calculated (Camerik and Werger, 1980):

Degree of sclerophylly, defined as the leaf dry mass per unit (bifacial) leaf area (g dm^{-2}).

Degree of succulence defined as the maximal water content of the leaf per unit (bifacial) leaf area (g dm^{-2})

We did not use Loveless' (1962) index of sclerophylly (per cent crude fibre plus per cent crude protein) as it would be of doubtful value in distinguishing between orthophyll and succulent leaves.

Direct gradient analysis

The vegetation transects were located in the Gamtoos river valley (S33° 50', E 24° 55'), from near the village of Hankey on the valley floor to near

TABLE 2.
Vegetation data for stations on the Gamtoos gradient. (A = low altitude station, E = high altitude station)

Station	Vegetation type	Vegetation structure ¹	Dominant species
FYNBOS	A Coast Renosterveld, Dry Grassy Fynbos	Low Mid-dense Small-leaved Shrub- land with a Mid-dense Grassy Understorey	<i>Elytropappus rhinocerotis</i> , <i>Themeda</i> <i>triandra</i> , <i>Erica decipiens</i> , <i>Merxmuellera</i> <i>stricta</i>
	B Grassy Fynbos	Low Mid-dense Ericoid Shrubland with a Mid-high Sparse Proteoid Shrub Overstorey and a Mid-dense Grassy-Restoid Understorey	<i>Protea neriifolia</i> , <i>Themeda triandra</i> , <i>Restio triticus</i> , <i>Erica pectinifolia</i>
	C Dry Proteoid Mountain Fynbos	Low Mid-dense Heathland with a Mid-high Mid-dense Proteoid Shrub Overstorey and Mid-dense Restoid Understorey	<i>Leucadendron eucalyptifolium</i> , <i>Hypo-</i> <i>discus striatus</i> , <i>Protea neriifolia</i> , <i>Restio</i> <i>triticus</i>
	D Dry Proteoid Mountain Fynbos, Proteoid Moun- tain Fynbos	Low Mid-dense Heathland with a Tall Open Proteoid Shrub Over- storey and a Mid-dense Restoid- Cyperoid Understorey	<i>Leucadendron eucalyptifolium</i> , <i>Protea</i> <i>eximia</i> , <i>Hypodiscus striatus</i> , <i>Tetraria</i> <i>compressa</i>
	E Proteoid Mountain Fynbos	Closed Restioid with Tall Open Proteoid Shrub and Low Sparse Heath Overstoreys	<i>Leucadendron loerense</i> , <i>Erica copiosa</i> , <i>Hypodiscus snyderi</i> , <i>Thamno-</i> <i>chorius argenteus</i>

Station	Vegetation type	Vegetation structure ¹	Dominant species
NON-FYNBOS	A	Succulent Thicket	Mid-high Closed Large-leaved and Succulent Shrubland
	B	Succulent Thicket	Tall Closed Large-leaved and Succulent Shrubland with an Open Herbaceous Understorey
	C	Thicket	Tall Closed Large-leaved Shrubland with a Low Sparse Large-leaved Tree Overstorey
	D	Afro-montane Forest	Low Forest with a Tall Open Tree Overstorey
	E	Afro-montane Forest	Tall Forest with a Low Mid-dense Tree Understorey
			<i>Portulacaria afra</i> , <i>Pappaea capensis</i> , <i>Euclea undulata</i> , <i>Brachylaena ilicifolia</i> <i>Euphorbia grandidens</i> , <i>Sideroxylon inerme</i> , <i>Euclea undulata</i> , <i>Aloe ferox</i> <i>Euclea undulata</i> , <i>E. schimperi</i> , <i>Pteroclastrus tricuspidatus</i> , <i>Sideroxylon inerme</i> <i>Rapanea melanophloeos</i> , <i>Podocarpus falcatus</i> , <i>Canthium inerme</i> , <i>Brachylaena glabra</i> <i>Gonioma kamassi</i> , <i>Ocotea bullata</i> , <i>Olea capensis</i> ssp. <i>macrocarpa</i> , <i>Podocarpus latifolius</i>

¹ Structural characterisation according to Campbell, Cowling, Bond and Kruger (1981).

the summit of the Elandsberg mountains, some 500 m higher. It was possible to place transects from approximately sea-level to 500 m in fynbos and non-fynbos vegetation. Corresponding stations were located at approximately 100 m intervals on each transect and at each station four 100 m² samples were randomly placed on different aspects (N, S, E, W). All slopes were uniformly moderate (8–16°). In each sample a full floristic list was made and the projected canopy cover and selected structural features for all species were noted. Leaf consistence was determined subjectively. Some floristic and structural data for transect stations are shown in Table 2.

Climate diagrams from three stations along the gradient are shown in Figure 1. The extremes of the gradient represent two distinct climates. Hankey has the typical valley climate of coastal plain valley bottoms in the south eastern Cape. Temperatures are generally higher than adjacent coastal mountain and maritime areas. These areas also have greater absolute maxima (40°C) and lower minima (−1,1°C) and greater diurnal variation throughout the year (see Louw, 1976). Monthly relative humidities are also lower, particularly during the warmest part of the day (Louw, 1976). Valley areas receive considerably less precipitation than adjacent mountains largely because they miss a great deal of post-frontal orographic rain from S and SSW winds and frontal rain associated with W and SW winds. Rainfall is also highly variable from year to year and may fall in any month although long-term averages do indicate spring and autumn maxima (Fig. 1).

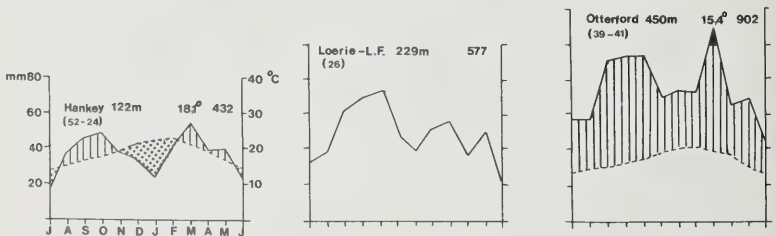


FIG. 1

Walter-Lieth climate diagrams (mean monthly air temperatures and rainfall) for stations on the Gamtoos transect. Temperature data adapted from climatically similar nearby station. (Uitenhage (108 m; 52 y) for Hankey, Van Stadens (452 m; 39 y) for Otterford). Hankey is representative of Stations A–B, Loerie Lower Forest of Station C, and Otterford of Station E. Data from S.A. Weather Bureau and Department of Forestry.

The coastal mountain climate (Otterford) is cooler, wetter and less variable on a daily and annual basis than the valley. Cool marine air keeps the temperatures equable although "berg wind" conditions may result in tem-

peratures of 39 °C, and frost and snow are occasional in winter (Forestry Department, pers. comm.). Rainfall is high (900 mm) and falls in every month of the year with peaks in spring and autumn (Fig. 1).

The transects are interpreted as representing gradients of increasing rainfall and decreasing temperature and decreasing climatic variability. The reliability of available soil moisture is likely to improve with increasing altitude.

At each station a topsoil sample was collected from a north and south slope. Air dried soil samples were analysed for texture, pH and macronutrients by staff of the soil laboratory, Department of Agriculture and Fisheries, Winter Rainfall Region (Stellenbosch). Soil data are shown in Table 3.

RESULTS AND DISCUSSION

Consistence determinations

Results showing leaf characteristics of species are given in Table 4. It is important to restrict comparisons among consistence types to leaves of the same size category since both degree of sclerophylly and succulence show significant positive correlations with leaf size (Camerik and Werger, 1980). The degree of sclerophylly ranged from 0,02 to 1,50 gdm⁻² (Table 4). Camerik and Wergers' (1980) values for a tropical high mountain flora ranged from 0,29 to 1,19 gdm⁻² and they quote Müller Stoll (1947-48) as considering species with values of 0,7 gdm⁻² and higher as true xerophytes. Within our sample all species classed as sclerophyll exceeded this value, except for the leptophylls. Within the sclerophyll group, however, leaf size was positively correlated with the degree of sclerophylly ($r = 0,87$ $P < 0,01$). Orthophylls, and to a lesser degree fleshy leaves, had lower values while those for succulents were comparable to the sclerophylls.

Degree of succulence was highest for succulents and second highest for fleshy leaves. The values of typical succulents are in the range 5,1-14,9 gdm⁻² (Kluge and Ting, 1978) which encompasses the values of both species classed as succulents in Table 4.

Figure 2 indicates that degree of sclerophylly and degree of succulence can be used to distinguish leaf consistence categories and lends some credence to the subjective scheme.

Direct gradient analysis

The relative importance of leaf consistence along the gradient, in fynbos and non-fynbos vegetation, is shown in Figure 3. The succulent category includes stem succulents (where the stem is the major photosynthesising organ and therefore the physiological leaf) and herbaceous succulents. In both fyn-

TABLE 3.
Soil data for stations on the Gamtoos gradient. N refers to soil samples from north slope, S at south slope; all samples from top-soil (150 mm)

Station	Parent Material	Texture ¹	S-Value ² (Meq %)	Total N ³ (%)	Available P ⁴ (ppm)	pH ⁵
FYNBOS	A Enon conglomerate	N Sandy loam	7,1	0,215	8,0	4,6
	B Enon sandstone	S Sandy loam	1,5	0,058	2,0	4,2
	C Enon sandstone	N Sandy loam	2,3	0,061	2,0	4,8
	D Table Mountain Sandstone	S Loamy sand	3,5	0,098	3,0	4,7
	E Table Mountain Sandstone	N Loamy sand	4,9	0,084	2,0	4,8
		S Loamy sand	4,3	0,073	3,0	4,8
NON-FYNBOS	A Bokkeveld shale	N Loam	9,2	0,181	25,0	3,9
	B Enon mudstone	N Sandy clay loam	7,8	0,157	9,0	4,5
	C Cango limestone, phyllite	S Sandy clay loam	30,4	0,200	11,0	7,0
	D Cango quartzite, ⁶ phyllite	N Loam	13,9	0,226	4,0	5,7
	E Table Mountain ⁶ Sandstone	S Loam	27,1	0,431	10,0	6,5
		N Sandy loam	8,8	0,389	25,0	4,5
		S Loam	4,4	0,201	11,0	3,7
		N Sandy loam	3,1	0,603	14,0	3,1
		S Loam	8,9	0,418	8,0	3,6

¹Texture determined by the standard hydrometer method. Texture classes according to MacVicar *et al.* (1977).

²Sum of exchangeable Ca, Mg, Na and K. Cation determinations made on 0,5 M NH₄Cl extract by atomic absorption spectro-

³photometry.

⁴Total nitrogen determined by the Kjeldahl method.

⁵Available phosphorus on a Bray No. 2 extract.

⁶pH measured in 1:2,5 N KCl (soil to solution ratio).

⁶Colluvial deposits.

TABLE 4.
Leaf characteristics. Leaf consistence determined by "feel" (see Table 1); leaf size category according to Raunkjær (1934). Results are the means of 10 separate leaves $\pm$ standard deviations.

Leaf Texture	Species	Leaf size Category	Average Leaf size (cm ²)	Degree of Sclerophyll (g dm ⁻²)	Degree of Succulence (g dm ⁻²)
Orthophyll	<i>Pelargonium zonale</i>	mesophyll	42.9 $\pm$ 8.7	0.44 $\pm$ 0.05	1.87 $\pm$ 0.22
	<i>Gardenia thunbergii</i>	microphyll	6.7 $\pm$ 0.6	0.19 $\pm$ 0.04	0.69 $\pm$ 0.05
	<i>Polygala myrsinifolia</i>	nanophyll	1.9 $\pm$ 0.2	0.28 $\pm$ 0.09	1.33 $\pm$ 0.24
	<i>Asparagus scandens</i>	nanophyll	0.22 $\pm$ 0.01	0.02 $\pm$ 0.01	0.31 $\pm$ 0.03
Sclerophyll	<i>Anthospermum aethiopicum</i>	leptophyll	0.11 $\pm$ 0.02	0.02 $\pm$ 0.01	0.04 $\pm$ 0.01
	<i>Protea compacta</i>	mesophyll	22.2 $\pm$ 1.4	1.50 $\pm$ 0.06	0.91 $\pm$ 0.06
	<i>Cassine peragua</i>	microphyll	15.8 $\pm$ 1.1	0.72 $\pm$ 0.03	1.27 $\pm$ 0.04
	<i>Carissa bispinosa</i>	microphyll	6.4 $\pm$ 0.4	0.84 $\pm$ 0.07	1.42 $\pm$ 0.14
Sclerophyll	<i>Olea europaea</i>	microphyll	4.7 $\pm$ 0.7	0.75 $\pm$ 0.05	1.08 $\pm$ 0.05
	<i>Metastasia muricata</i>	leptophyll	0.18 $\pm$ 0.04	0.35 $\pm$ 0.02	0.70 $\pm$ 0.07
	<i>Erica phyllicaefolia</i>	leptophyll	0.17 $\pm$ 0.02	0.33 $\pm$ 0.06	0.51 $\pm$ 0.08
	<i>Osteospermum ecklonis</i>	microphyll	5.1 $\pm$ 0.5	0.31 $\pm$ 0.04	2.36 $\pm$ 0.13
Fleshy (semi-succulent)	<i>Chrysanthemoides monolifera</i>	microphyll	4.8 $\pm$ 0.6	0.63 $\pm$ 0.01	2.01 $\pm$ 0.27
	<i>Salvia africana</i>	nanophyll	1.4 $\pm$ 0.1	0.36 $\pm$ 0.03	2.53 $\pm$ 0.18
	<i>Eriocephalus africanus</i>	leptophyll	0.18 $\pm$ 0.02	0.30 $\pm$ 0.06	1.85 $\pm$ 0.17
Succulent	<i>Portulacaria afra</i>	nanophyll	1.2 $\pm$ 0.1	0.89 $\pm$ 0.02	7.52 $\pm$ 1.93
	<i>Lampranthus multicaulis</i>	nanophyll	0.48 $\pm$ 0.02	0.54 $\pm$ 0.03	12.07 $\pm$ 2.12

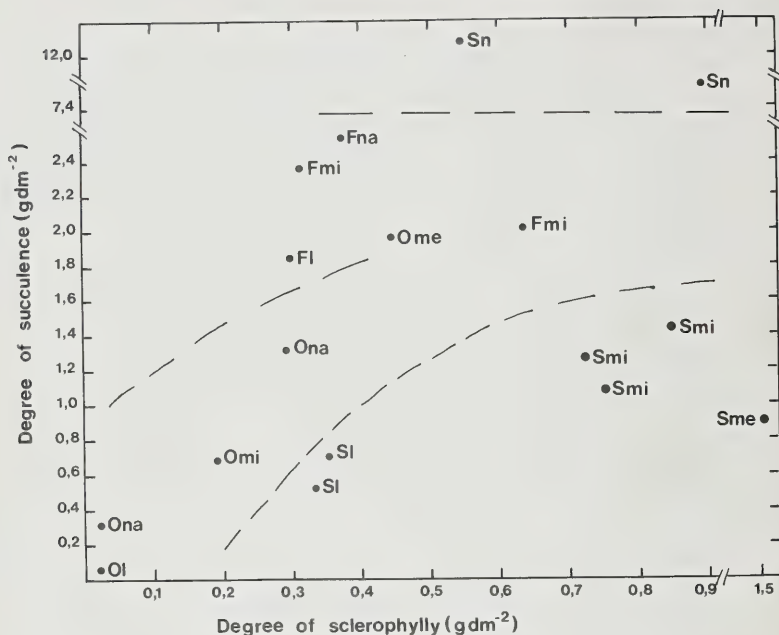


FIG. 2.

Scatter diagram showing relation of subjectively determined leaf consistence for 17 species to degree of sclerophyllity and succulence. S = sclerophyll, O = orthophyll, F = fleshy, Sn = succulent, l = leptophyll, na = nanophyll, mi = microphyll, me = mesophyll.

bos and non-fynbos the contribution of deciduous species to total cover was negligible (0–5 % relative percentage cover).

Succulents and fleshy leaves

There is little doubt that the storage of water by plants represents an ecological adaptation; the plant is able to overcome periods of water deficiency with endogenous water reserves (Kluge and Ting, 1978). It would be desirable, though not possible in this study, to correlate succulence with the crassulacean acid metabolism (CAM) mode of carbon gain since the adaptive significance of CAM is well understood (Kluge and Ting, 1978). A high degree of succulence is, in itself, not a criterion for CAM; only those succulents which unify the sites of malic acid synthesis, storage and conversion within the same cells, can be expected to have CAM (Kluge and Ting,

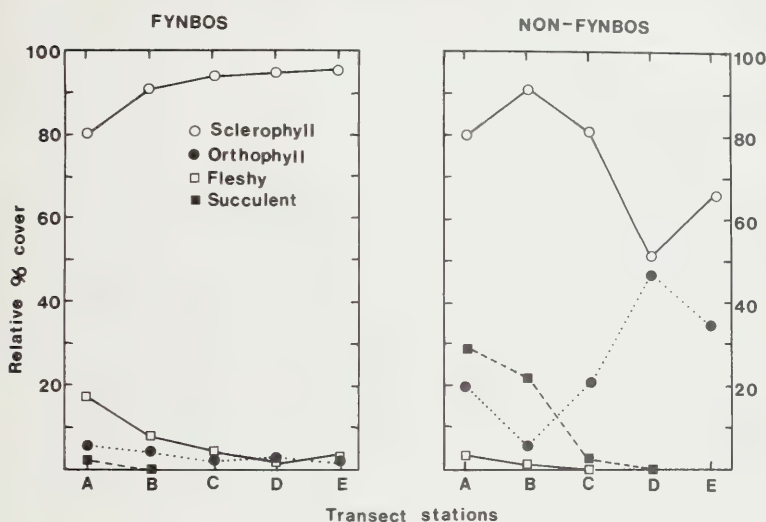


FIG. 3.

Importance of leaf consistence categories along an altitudinal gradient in fynbos and non-fynbos vegetation in the Gamtoos river valley. Succulents expressed as a percentage of total cover; other categories expressed as a percentage of total woody cover. Results are the mean values of four 100 m² samples at each station.

1978). In our study area most of the predominant succulent genera (*Euphorbia*, *Crassula*, *Portulacaria*, *Delosperma*, *Aloe*, *Senecio*) are known to possess CAM (Mooney, Troughton and Berry, 1977), while another (*Zygophyllum*) is non-CAM (Kluge and Ting, 1978).

CAM succulents are extremely economical in terms of the ratio of carbon gained to water lost but have associated costs of low rates of carbon fixation and are not competitive where soil moisture is not limiting for extended periods (Ting and Szareck, 1975; Kluge and Ting, 1978).

Predictably succulents had maximum cover in the low altitude valley climate areas (Fig. 3) with low unpredictable rainfall. Valley regions also experience great diurnal temperature fluctuations. It has been shown that optimum growth of some CAM species occurs under conditions of low night (10–15 °C) and high day (25–30 °C) temperatures (Neales, 1973; Osmond, Bender and Burris, 1976).

In fynbos fleshy leaves largely replace succulents at the xeric end of the gradient. They are common at corresponding non-fynbos sites with more

fertile soils (Table 3) (cf. Bond, 1981). As yet, the water relations and carbon gaining mechanism of fleshy plants have not been studied.

Sclerophyll and orthophyll leaves

There are two major hypotheses to explain the relative fitness of sclerophyll leaves to a particular habitat. The "drought" hypothesis, originally stated by Schimper (1903) is best articulated by Orians and Solbrig (1977). Sclerophylly has also been interpreted as a response to low levels of nutrients, particularly nitrogen and phosphorus (e.g. Loveless, 1962).

Orians and Solbrig (1977) have developed a descriptive cost-income model which takes into account water loss and carbon gain as well as morphological and physiological traits that affect these processes. Sclerophyllous leaves are interpreted as "high cost-slow profit" structures which are able to withstand high negative leaf water potentials through the development of energetically expensive supporting structures. These and other biochemical changes apparently restrict high photosynthetic rates when water is available (see Orians and Solbrig for supporting data) but allow the plant to yield profits when more mesophytic leaves have become an energetic liability. Sclerophyllous leaves are mostly longlived.

Orthophyll leaves ("low cost-quick profit") are cheaper to build and maintain per unit surface area and yield profits at faster rates than sclerophyllous leaves, provided soil water potential is low. As negative soil water potential builds up they cease to yield profits but maintenance costs continue, resulting in a net loss in keeping the leaf (Orians and Solbrig, 1977). It is clearly beneficial to drop leaves under these conditions.

This model predicts that sclerophyllous leaves are at a competitive advantage where periods of high soil moisture availability are short and erratic (e.g. semi-desert) or do not coincide with the growing season (e.g. mesic mediterranean climates (Miller, 1982; Mooney, 1982)). Orthophyll leaves will be favoured in tropical savanna, tropical rain forest and temperate broadleaf forest climates (Orians and Solbrig, 1977). We would expect, therefore, a predominance of sclerophylly at the xeric end of the Gamtoos gradients, with orthophylls becoming increasingly important towards the higher altitudes.

With some discrepancies this is the trend in the non-fynbos communities (Fig. 3). The trend observed for the fynbos communities does not agree with the predictions made by Orians and Solbrig's (1977) model. Here sclerophyll leaves predominate throughout the length of the gradient (Fig. 3). This cannot be explained by the soil moisture hypothesis alone; rather we interpret it as a response to the low fertility of fynbos soils (Table 3).

In recent years evidence has accumulated to support the hypothesis that

a sclerophyllous leaf is the expression of a metabolism found in plants that can tolerate low levels of certain nutrients, particularly phosphorus (Loveless, 1962; Beadle, 1966; 1968; Small, 1972; 1973; Steurbing and Alberdi, 1973). Loveless (1962) suggests that the excessive fibre contents typical of sclerophyllous leaves is due mainly to an absence of adequate phosphate. Thus products of metabolism which otherwise might have formed protein, are diverted along alternative metabolic pathways to form other end products, such as fibre. It is therefore possible to view sclerophylly on infertile soils, particularly in areas where soil moisture is not limiting, as a non-adaptive feature determined by "biochemical" constraints (Gould and Lewontin, 1979) imposed on the leaf by a metabolism associated with limiting amounts of certain nutrients. On the other hand, adaptive advantages can be inferred, especially for both arid and infertile environments (Small, 1973). Small's (1973) hypothesis that there should be a degree of overlap in the ecological amplitude of plants adapted to arid and infertile environments is rejected for the Gamtoos transects since there are no species common to the xeric non-fynbos stations and the fynbos transect.

In conclusion it appears that patterns in the relative importance of leaf consistence in non-fynbos communities on relatively fertile soils, can be interpreted largely in terms of soil moisture and climatic factors; in fynbos communities low levels of soil nutrients may be of overriding importance in determining leaf consistence.

ACKNOWLEDGEMENTS

We thank Sue Painting and Wendy Lloyd for valuable laboratory assistance. R.M.C. collected the Gamtoos field data. This study was funded by the CSIR (R.M.C.), the Botanical Research Institute (B.M.C.) and is part of the Fynbos Biome Project. W. Bond, M. Werger and W. Westman made useful comments on an earlier draft.

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